AUSTRALASIAN CERATOPOGONIDAE (DIPTERA, NEMATOCERA).

PART I. RELATION TO DISEASE, BIOLOGY, GENERAL CHARACTERS AND GENERIC CLASSIFICATION OF THE FAMILY, WITH A NOTE ON THE GENUS CERATOPOGON.

By David J. Lee, B.Sc.

(With 23 Text-figures.)

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Contents.

The present paper is the first of a series designed to revise and extend our knowledge of Australasian Ceratopogonidae. As some sections of this work have been complete for some time and others have been delayed by extensive additions to the basic material, it has been decided to present the revision in a series of parts, each of which is to be as complete as available material and data permit.

Introduction.

In common with other blood-sucking insects the Ceratopogonidae have at times come under suspicion as vectors of disease. The earliest such suggestions in Australian literature concern worm nodule in cattle, caused by the filarial worm *Onchocerca gibsoni*. Cleland, Dodd and Ferguson (1916) mention *Culicoides molestus* as being numerous on Milson Island in the Hawkesbury River (New South Wales), whereon they conducted their experiments, and although they record this species as often swarming about the ears of cattle, they discount the possibility of its being the vector. Similarly Dickinson and Hill (1916) list *Culicoides subnitidus* (now *Forcipomyia subnitida*, but this is not likely to have been a correct determination) as one of the biting flies taken in the vicinity of their laboratory at Fanny Bay (Northern Territory), but again do not attach any significance to this finding. There is now, of course, far more reason to suspect a ceratopogonid as the vector of *Onchocerca gibsoni*, since Steward (1933) has shown *Culicoides nubeculosus* to be the vector of *Onchocerca cervicalis* of horses in England, and more recently Buckley (1938) has produced evidence that certain species of *Culicoides* are the vectors of *O. gibsoni* in Malaya. He

found natural infections in *Culicoides* spp. and obtained experimental infections in these insects with a very low percentage of parasitism but was not able to demonstrate actual transmission to cattle.

Elsewhere *Culicoides austeni* and *C. grahami* are known to transmit the filarial parasite *Acanthocheilonema perstans** in Africa (Sharp, 1928), and *C. furens* transmits *Mansonella ozzardi* in South America (Buckley, 1933, 1934).

Apart from their role as vectors of filarias, sandflies† have long been known as irritating and persistent pests of man and domestic animals wherever they may be locally abundant. In Australia this is particularly true of coastal mangrove areas in the vicinity of which the densest sandfly populations are found, but one may be subject to their attacks in a much wider variety of situations. The actual bite is not always noticed by the victim; indeed only particularly susceptible people seem to be immediately aware of the bite, but irritation usually sets in within a few to 24 hours after the time of biting. The irritation may last with decreasing potency for several days, but in some individuals a local toxic condition at the site of the bites may persist for weeks.

When, in 1936, the author was collaborating in experiments designed to discover the vector of ephemeral fever of cattle in Australia, sandflies came under suspicion.‡

Just prior to the outbreak of war in 1939 the first attempts at experimental transmission through the agency of sandflies were made by Dr. I. M. Mackerras at Canberra, using sandflies collected by the author from cattle in Central Queensland. Unfortunately these had to be discontinued even before satisfactory techniques for handling these small insects could be devised.

However, it was soon clear, in these very preliminary studies, that so little was known of the Ceratopogonidae in Australia that it was practically impossible to identify any specimens collected in the field, that not a single life history was known and very little was known of the distribution or habits of any Australian species. In 1936 some preliminary studies of the taxonomy of this group were carried out, together with field observations in the vicinity of Sydney and in Central Queensland. It was soon clear that this particular family of flies was far more common than was previously suspected, and that even in areas where they were not known to occur, even by the local inhabitants, they might still be found in large numbers feeding on cattle. These preliminary studies had then to be broken off and it was not until 1946 that the author was able to give some further attention to this group, the results of which are presented below.

Acknowledgements.

I am deeply indebted to the late Mr. A. L. Tonnoir for his assistance in the early stages of this work and for the loan of his Ceratopogonid collection (now the property of the Division of Economic Entomology, Council for Scientific and Industrial Research, Canberra, A.C.T.).§ Indeed without this collection, although only representative of

* Recent texts on Tropical Diseases mention *A. perstans* as occurring, or possibly occurring, in New Guinea. The only evidence for such a statement appears to be a record published by Manson in 1892 which has not been verified or corroborated by later observations. Whether or not the record is true must remain in doubt at present, but the evidence is obviously very slender. Actually, Manson in 1900 (Tropical Diseases, first edition), stated that he had never found *F. perstans* outside of Tropical West Africa and in aborigines of Demarara, but that he had found a microfilaria closely resembling *F. demarquaii* in the blood of natives of New Guinea. Now of course *F. demarquaii* is regarded as a synonym of *M. ozzardi*. All that can now be said is that an unsheathed microfilaria has been found in natives of New Guinea which has not yet been adequately identified.

† The term sandfly is used in Australia for both Ceratopogonidae and Simuliidae. Here, of course, only the former are referred to by this term. Further confusion is likely to arise with the sandflies of the Middle East, which are Psychodidae of the genus *Flebotomus*.

‡ The evidence which may be offered implicating Ceratopogonidae in the transmission of ephemeral fever has been reviewed by Mackerras and Mackerras (1940, p. 108) and Seddon (1938).

§ Most of the material examined, including type series, has been lodged in the Museum of this Institution, which is referred to as the C.S.I.R. Museum in later parts of this series.

Tasmania and the Australian Capital Territory, it would not have been feasible to initiate this present revision.

Other material has been supplied by the School of Public Health and Tropical Medicine, University of Sydney, and I would also like to express my particular gratitude to Messrs. R. H. Wharton, who has assisted me in collecting a large amount of material, J. Henry, who has collected a valuable series of specimens in the vicinity of Sydney, and M. M. H. Wallace, who has provided useful material from both New Guinea and Western Australia. Throughout the series will appear numerous photographs of wings, the excellence of which is due entirely to the skill of Mr. E. Parrish, of the C.S.I.R. McMaster Laboratory, University of Sydney. The co-operation of Mr. Parrish was made possible through the kind offices of Mr. D. A. Gill, Officer-in-Charge, McMaster Laboratory, and Dr. A. J. Nicholson, Chief, Division of Economic Entomology, C.S.I.R., Canberra.

The Family Ceratopogonidae.

Family Status.

Most authorities have regarded the Ceratopogonidae as merely a subfamily of the Chironomidae, but following Malloch (1917) and Edwards (1926) it is considered that full family status should be accorded to the group. A tabulation of differential characters between the Chironomidae and the Ceratopogonidae is to be found in Edwards (1926).

General Characters of the Ceratopogonidae.

Members of the family Ceratopogonidae are differentiated from those of other families of nematocerous diptera by their small to minute size and compact body with relatively short, strong legs, wings of the same length as the abdomen, prominent chitinized mouthparts extending as a piercing organ ventrally from the head and approximately equal to the height of the head in length and antennae usually as long as or longer than the thorax. The resting attitude is such that the long axis of the head (continuing the line of the mouthparts) is almost at right angles to the long axis of the body and the wings are folded flat over the body, the one lying on top of the other.

Recognition in the field depends to some extent on an appreciation of the characters mentioned above but is, of course, considerably simplified when most of the other groups of small nematocerous flies can be eliminated by immediate recognition. With some practice the general appearance of sandflies may be appreciated to the extent that very little confusion occurs in their field collection, a few Mycetophilidae, small species of Chironomidae and occasional small Phoridae being all that may be mistakenly collected.

Identification under the microscope is relatively simple with Australasian species, since they are the only flies in which all branches of the reduced radius meet the costa before the apex of the wing and usually about the centre of the anterior margin, enclosing one or two radial cells, with both M_1 and M_2 present and the $M_{3+4} - Cu_1$ fork near the middle of the wing. These wing characters, in conjunction with the shape of the antennae, which are moderately long with from the last one to the last six obviously longer than the basal flagellar segments and the chitinized piercing mouthparts, serve to distinguish the group.

It is at present rather more difficult to characterize the larvae of the Ceratopogonidae, since there are a number of distinct types. However, in all except the *Leptoconops* group there is a distinct chitinized head capsule and the thorax is differentiated into three segments. In most the body tapers distinctly to both ends and some are apparently smooth without any obvious external structures and others have lateral and/or dorsal chitinous prolongations or setae. Some have a pair of prothoracic prolegs and a pair of posterior prolegs (on anal segment), others only a posterior pseudopodium. The majority of larval forms fall within these types which will be found defined in more detail below.

Less difficulty should be occasioned in the recognition of the pupae. These are obviously divided into a cephalothoracic region and a segmented abdomen, both regions being strongly chitinized. The paired breathing horns arise laterally at or near the anterior end, and on the abdominal segments there are strongly chitinized angles or prolongations laterally, and the terminal segment has a pointed prolongation on each postero-lateral angle. The pupae are capable of restricted movement only and may be free from the larval exuvium or with the latter surrounding the distal portion of the body.

Habits.

Although the most commonly known species are those whose adult females suck the blood of man, others attack other vertebrates. *Culicoides* and *Leptoconops* and related genera are particularly well known for their anthropophilic species. Other groups are recorded as sucking a wide variety of insects such as Chironomidae, Culicidae, Lepidoptera and Coleoptera and even other Ceratopogonidae. One genus, *Pterobosca*, has only been taken from the wings of Odonata. Kieffer (1925) also mentions that large numbers of adults, almost invariably females, may at times be taken from the flowers of various Umbelliferae.

Blood-sucking adults may be collected by exposing oneself to attack under suitable conditions. Sandflies are known to bite at almost any time of the day (some are recorded as nocturnal), particularly when there is a very dense population of these insects. Where they are not present in large numbers a combination of warm moist conditions without wind will often disclose them biting in the very early morning or late afternoon. Animals such as cattle, horses or dogs may often attract species which pay little attention to humans. Predatory species may be collected by sweeping vegetation with a fine net in areas adjacent to probable breeding sites (pools, streams and so on) or by picking them from the vegetation individually once one has learnt to distinguish their general shape from other types of small Diptera. Large numbers of sandflies are at times attracted to lights in bush areas and this has proved a useful method for collecting species of *Forcipomyia*.

Nothing has yet been published concerning the larvae of Australian species. Searches by the author in mangrove areas have as yet failed to yield any Ceratopogonid larvae or pupae but both stages of several species (of *Culicoides* and *Dasyhelea*) have commonly been found in small rock pools in both coastal and mountain streams in the Sydney district and in rather similar situations in Central Queensland.

Elsewhere in the world the recorded larval habitats are very various, ranging from wet sand between tide levels through wet, muddy areas to pools in streams, the margins of small lakes, dams and so on, often in blanket or filamentous algae; in tree holes; and also in moist decaying vegetation; under the bark of trees and even in the exudate from wounds in the holes of trees such as maple and elm. A few species have also been recorded in the nests of ants. Obviously, then, much has still to be discovered concerning the life histories of Australian species.

Detailed Characters of the Family.

Although the present series is to be largely devoted to the systematics of the Ceratopogonidae, with particular reference to adults, brief characterization of eggs, larvae, and pupae have been included to assist any new student of the group in recognizing these stages.

Eggs.

These have not been seen by the author, but they may resemble those of the Chironomidae in being laid in masses, some in long ribbons, others in compact groups. Other species are recorded as ovipositing singly. The individual eggs are elongate and cylindrical, usually straight, but those of *Dasyhelea* are horseshoe-shaped.

Larvae.

The following information is a condensation of that contained in Goetghebuer (1920), Kieffer (1925) and Thomsen (1937). There is general agreement that there

are three recognizable forms assumed by the larvae which correspond to three corresponding pupal forms and to a lesser extent to adult groupings.

The first grouping is that in which the larvae possess a pair of anterior prolegs ventrally on the prothorax and another pair of posterior prolegs on the anal segment. The body is not vermiform but has the dorsal surface covered with at least short setae which may be modified into variously formed appendages. The mandibles are directed ventrally. This group comprises the larvae of *Forcipomyia*, *Atrichopogon* and closely related genera.

In the second group no anterior prolegs are present but there is, however, a retractile anal pseudopodium. The body is vermiform and lacks any distinct setae or modified structures. The mandibles are also directed ventrally. To this group belong the larvae of *Dasyhelea*.

The third group lacks all prolegs or pseudopodia, the body is also vermiform, without appendages, and the mandibles in this case are forwardly directed. Members of this group comprise *Culicoides* and the *Palpomyia*, *Stilobezzia* and *Bezzia* groups of genera.

In addition, however, a fourth grouping must be contemplated to include the larvae of *Leptoconops* and its allies, about which very little is yet known. Thomsen (1937) indicates that prothoracic prolegs are lacking and that "the head is not sclerotized, but provided with a system of heavily sclerotized rods and levers", this information coming from Painter (1926).

Pupae.

The general appearance of the pupae has been detailed above. Three groups of pupal forms are to be correlated with the first three larval groups mentioned above.

Those of the first larval group (*Forcipomyia*, *Atrichopogon* and related genera) have the thoracic trumpets usually arising from a stalk and swollen distally with a sinuous distal margin bearing the spiracular openings or else the trumpet rather strongly resembles an ear. The posterior portion of the abdomen is held within the cast larval skin.

Species of the second group (*Dasyhelea*) and also the third have the pupae free of the larval exuvium but may be differentiated by the form of the posterior border of the apical segment (between the spines). In the second group a pair of small tubercles from which a minute hair arises is found on this margin, whereas species of the *Palpomyia*, *Culicoides*, *Bezzia* and *Stilobezzia* groups lack these structures.

Adults.

A number of papers on the Ceratopogonidae [viz., Carter, Ingram and Macfie (1920), Goetghebuer (1920), and Kieffer (1925)] include fairly detailed accounts of the anatomy of these flies and also include many useful explanatory figures. The following account emphasizes the characters found most useful in a study of Australasian species, but an attempt has also been made to indicate the differential characters of other groups not as yet found in the Australasian region.

Size: The variation in size is rather wider than one only accustomed to the small anthropophilic species would imagine, and in known Australian species there is a range of body length (head to tip of abdomen) of from about 1·0 mm. to 3·5 mm. and in wing length from 0·8 mm. to almost 4·5 mm.

Head: The head is subglobular, the anterior face being rather characteristically flattened, and this appearance is emphasized by the anterior surface being in line with the dorsal surface of the elongated mouthparts, the length of which is roughly equivalent to the height of the head and rarely only about one-fourth the height of the head. The dorsal surface of the head, comprising the posterior occiput and undifferentiated anterior vertex, is invested with scattered setae and a row of orbital bristles overhang the eyes. The eyes may be joined or separated by an inter-orbital space and, if separate, they are usually more widely spaced in the male than in the female. Some genera, e.g., *Atrichopogon* and *Stilobezzia*, appear to be characteristically

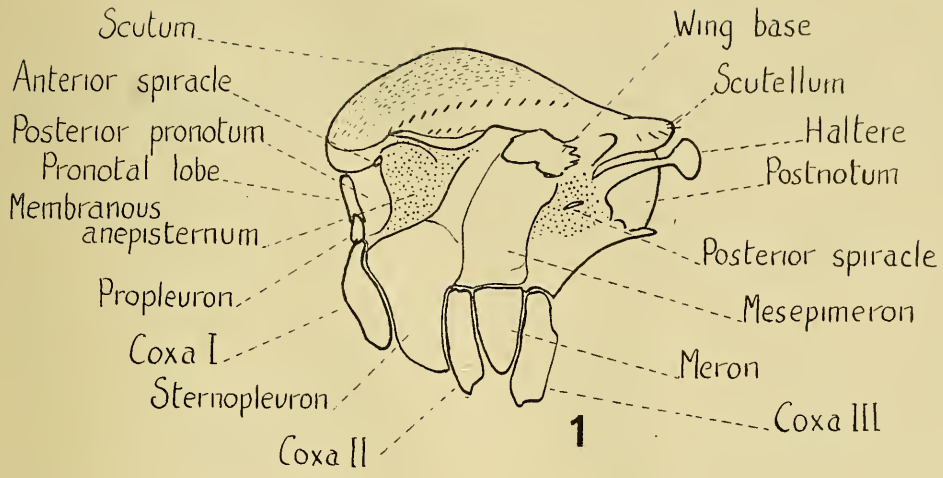
holoptic, and others, e.g., *Culicoides* and *Palpomyia*, usually have the eyes separated. In *Culicoides* the narrow inter-orbital area in the female bears a single strong seta just below the vertex (Text-figure 12), and this character may be useful in placing species whose generic position may be difficult to establish otherwise. In *Leptoconops* (sens. lat.) the eyes are far more widely separated than in any other group. The eyes themselves are usually bare but may be finely pubescent between the facets (as in *Dasyhelea*).

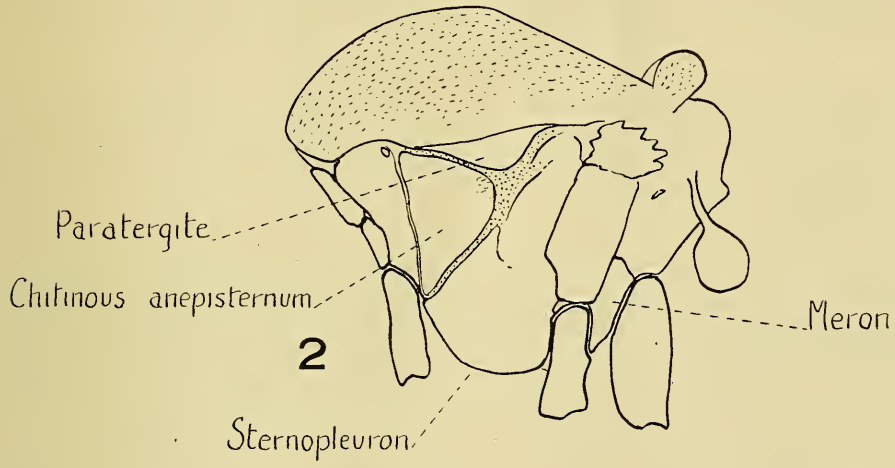
The antennae (Text-figure 12) comprise fifteen segments in most genera (a reduction to from twelve to fourteen segments occurs in *Leptoconops* and related genera), the first being usually reduced to a ring-like segment around the base of the enlarged second segment or pedicel, but in females of *Culicoides* the first segment may be almost as large as the second. The pedicels of the female are separated but in the male they are further enlarged and often touching. The flagellum then comprises thirteen segments, but the shape of the individual segments varies in different genera and furnishes useful diagnostic characters. The first eight flagellar segments of the female vary from transverse to cylindrical but are nearly always markedly shorter than the last five (or six in *Pterobosca*). In males usually the last four flagellar segments are elongated. (In the *Leptoconops* group of genera the antennae are somewhat similar to those of the *Simuliidae*, with very short flagellar segments, and in this group only the apical segment is elongated. See Text-figure 14.) There are sparse verticels on the flagellar segments of the female (usually reduced on the distal, differentiated segments) and the male has dense, applied verticels of very long hairs on the second to tenth flagellar segments. Occasionally, as in *Atrichopogon* the terminal antennal segment ends in a small stylet and in most species of *Dasyhelea* the integument of the antennal segments is sculptured (see Text-figure 17).

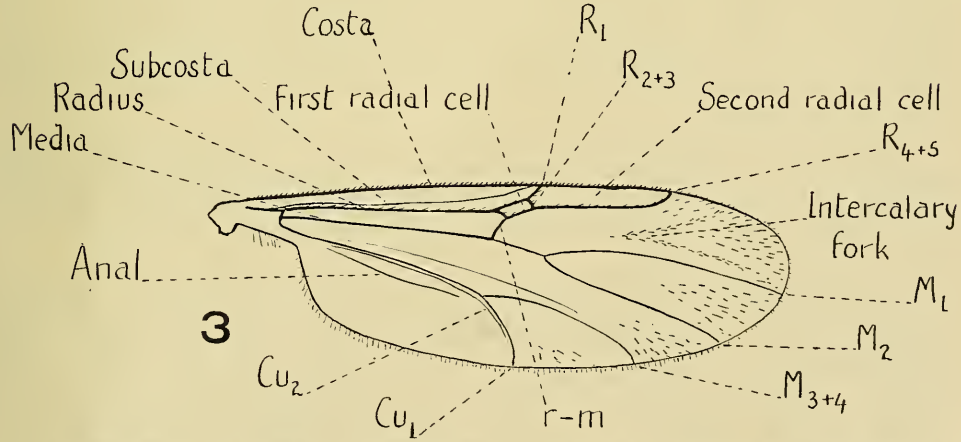
The mouthparts of the female are composed of seven distinct parts, the strong, apically toothed labrum, the paired maxillae and mandibles, both slender structures with distal serrations, those of the maxillae being by far the most obvious; the tubular hypopharynx and the enclosing sheath or labium, which is hairy externally. In the male the mouthparts are somewhat shorter, the labium similar but narrower, and the other parts neither as strong nor as powerfully armed. The palpi are normally of five segments (reduced to four in *Leptoconops*) and of these the second and third are longer than the rest, and the third is often expanded distally around a sensory area.

Thorax: The thorax is rather squat, scarcely longer than broad, broadest anteriorly but not narrowing greatly until just before the scutellum. The anterior end is strongly arched but does not project over the head, and the prescutellar area is well marked as a flattened or lightly depressed, anteriorly rounded, laterally and posteriorly straight area. There may also be a pair of humeral pits (Text-figure 23) laterally near the anterior margin (*Culicoides*, *Stilobezzia*) or at the middle of the anterior margin a small spine may arise (*Palpomyia*). The surface of the scutum is variously adorned in different genera, sometimes it is glabrous, in others there is a distinct pattern resulting from the surface bloom (pruinescence). There may be a uniform covering of minute, pubescent hairs or there may be longitudinal rows of short setae. The pleura vary in the shape of the pleurites, the extent of chitinization of the anepisternum and the development of the meron, the variations being correlated with major divisions of the family (see below, page 324). Text-figures 1 and 2 illustrate the form of the thorax, in lateral view, as found in *Atrichopogon* and *Xenohelea*.

Legs: The legs are shorter and more thickset than in the Chironomidae. Many features of diagnostic importance are to be found in the legs, including the size of the femora (they may be considerably swollen in some species) and the presence or absence of spines on them, the ratios of the length of various segments, particularly those of the tarsi, the presence or absence of spines on the tarsal segments, the shape of the tarsal segments, particularly the fourth and fifth, the size and shape of the claws and the presence or absence of an empodium. It is sometimes important to differentiate between what are usually called spinules, that, is rather thick black, but tapering spines, and the stouter, blunt, non-tapering "batonnets".







Text-figures 1-3.—Text-figure 1. Lateral view of thorax of *Atrichopogon* sp. Text-figure 2. Lateral view of thorax of *Xenohelea* sp., with parts showing striking differences from *Atrichopogon* labelled. In both text-figures 1 and 2 membranous areas of the pleura are stippled. Text-figure 3. Wing of *Stilobezzia* sp. showing terminology of venation. Various magnifications.

Wings: Although the wings are particularly important in generic segregations, much confusion is caused by the various nomenclatures adopted for the venation. Text-figure 3 reveals the terminology used in this series following the Comstock-Needham system as interpreted for Nematocera by Tillyard, and Table 1 gives the corresponding

TABLE 1.

Wing Venation.

Symbol and Name Used in this Series.	Name Used by Kieffer.	Name Used by Skuse.
C. Costa.	Costal vein.	Costa.
Sc. Subcosta.	Subcostal vein.	Auxiliary.
R_1 Radius 1.	Radial vein.	First longitudinal.
R_{2+3}. Radius 2 and 3.	——	Marginal cross-vein.
R_{4+5}. Radius 4 and 5.	Cubital vein.	Second longitudinal.
r-m. Radio-median cross-vein.	Transversal.	Middle cross-vein.
Intercalary fork.	Intercalary fork.	Third longitudinal.
M_1. Media 1.	Anterior branch of discoidal vein.	Anterior branch of fourth longitudinal.
M_2. Media 2.	Posterior branch of discoidal vein.	Posterior branch of fourth longitudinal.
M_{3+4}. Media 3 and 4.	Anterior branch of postical vein.	Anterior branch of fifth longitudinal.
Cu_1. Cubitus 1.	Posterior branch of postical vein.	Posterior branch of fifth longitudinal.
Cu_2. Cubitus 2.	——	——
An. Anal.	Anal.	——

terminologies used by Skuse and Kieffer, the two major authors on Australian Ceratopogonidae. The outstanding features of the venation are the reduction of the radius and the termination of all its extant branches in the costa and the union of the radius to the media by a cross vein (except in *Leptoconops* and its allies). Points of particular importance concerning the venation are the length of the costa, the number of cells formed by the branches of the radius and the costa (one or two), the relative size of these radial cells, and the position of the base of M_2 in relation to the r-m cross vein. Sometimes a fork, the intercalary fork, is seen in the antero-distal section of the wing. Both microtrichia and macrotrichia may or may not be present on the wing membrane, and in some species the wings are densely clothed with recumbent, almost scale-like long hairs. In some species (particularly of *Culicoides*) the wings are spotted, this appearance being most marked when the wings are viewed by oblique lighting.

Abdomen: The abdomen is usually short and broad and blunt, but even if somewhat elongate, does not obviously exceed the length of the wings. The female abdomen terminates in a pair of short, rounded or pointed lamellae in most genera (they are excessively long in *Leptoconops*). The number and shape of the spermathecae are at times useful in classification.

Male Genitalia: These are simple, with, usually, the ninth tergite a large plate superimposed over the majority of the rest of the structures, and its internal and apical surfaces may be considerably modified. The coxites are simple, without accessory structures, except the terminal style, which is also usually simple. The harpes are paired sub-median structures (sometimes fused), which may be useful in specific diagnosis, and there is a median phallosome shaped like an inverted Y and there may be modifications at its distal extremity (the base of the Y). Rotation of the terminalia may be complete or incomplete.

General Systematics.

Previous Australian Literature.

Although over eighty species of Ceratopogonidae have been described or recorded from the Australasian Region (Australia, New Guinea and the Bismarck Archipelago, and New Zealand, other Pacific islands being excluded from the total) the problems of identification have remained extremely difficult. Many of these species were not described in the genera to which they would now be assigned. Many new genera have been defined since 1889, when Skuse described some seventeen species, all of which, with the exception of one, he placed in the genus *Ceratopogon*. Furthermore, Skuse ignored a number of generic names which were available at that time. Changes in generic concepts have also taken place even since Kieffer's description of a further twenty-five species in 1917. Since the latter date no one has paid any particular attention to this family in Australia except Carter (1921), who revised the genus *Leptoconops*, and Macfie (1939*b*), who revised the status of six species. Descriptions of individual species have been published from time to time by various authors, namely, Schiner (1868), Taylor (1911, 1918), de Meijere (1915, 1917) and Macfie (1939*a*). In recent years attention has been paid to New Zealand species by Ingram and Macfie (1931*a*) and Macfie (1932). Apart from *Leptoconops* nothing approaching a revision of even a single genus has previously been attempted.

Difficulties in Recognizing Genera.

The difficulties in working with this group are initially at the generic level. Kieffer's "Key for the Determination of Genera" (1926) separates some 59 genera and Macfie's "Key to Genera" (1940) separates 63 genera. However, 21 of the genera mentioned by Kieffer apparently fall into synonymy when revised by Macfie, and 24 of the genera listed by Macfie are not mentioned in Kieffer's key. This is clearly indicative of the state of flux of generic conceptions. A further difficulty arises in that many genera have not been adequately defined, although Edwards' (1926) revision of British species contains reasonably full generic diagnoses of the genera occurring in Great Britain. The absence of full generic definitions in Macfie's (1940) key to genera detracts from the usefulness of this work, although it is of value as a concise statement of his findings after many years of work with this group.

Naturally, when one tries to identify an Australian specimen generically, according to Kieffer's 1926 key, or Edwards' generic definitions of 1926, or yet again Macfie's 1940 key, the results from each attempt are not always in agreement. This is partly due to the fact that present generic distinctions are often artificial and based on trivial rather than fundamental characters. It does seem agreed that a comprehensive study of male genitalia characters would lead to a more natural and workable grouping of species, but this is a project for which much special collecting would be necessary in all zoogeographical regions. It does appear to the author, and there is some evidence that in the opinion of Edwards also, that the number of genera might be reduced considerably if they are to delimit reasonably natural groups. The adoption of some of the present genera as subgenera would certainly lend clarity to the systematics of the group, but any generic revision is undoubtedly the province of a worker with access to far more material than the present author.

In the following review, apart from the description of newly discovered species an attempt is made to identify generically all described species from Australia, New Zealand and New Guinea as well as to disclose the characters by which individual species may be recognized. When doubt arises as to what genus a particular species belongs an attempt is made to place it with the species to which it appears most closely related and about whose generic status there appears less doubt. A perusal of the literature reveals that more than one author has in the past been forced to place species in genera into the circumscription of which they do not really fit, but to which they appear to belong because of their apparently obvious relation to other species legitimately placed in such genera. Even Ingram and Macfie (1931*b*, p. 215) have had

TABLE 2.

Differentiation of the Ceratopogonidae into Groups on Characters found in the Larvae, Pupae and Male Genitalia.

Group *Culicoides.*	Group *Ceratopogon.*	Group *Stilobezzia.*	Group *Macropeza.*	Group *Palpomyia.*	Group *Bezzia.*
Present.	Not known to be present.	Present.	Not known to be present.	Present.	Present.
Culicoides.	——	*Stilobezzia, Acanthohelea, Monohelea.*	——	*Palpomyia, Clinohelea, Heteromyia, Xenohelea, Johannsenomyia, Dicrohelea.*	*Bezzia, Nilobezzia.*
Head capsule present; wide, oval; mouthparts reduced; anterior and posterior prolegs absent; last segment with bristles; body slender, round in cross-section; pharyngeal skeleton with about four combs, angulus of distinctly separate parts.	Not adequately known. In genus *Alluaudomyia* head capsule present; anterior and posterior prolegs absent; last segment with long setae; body slender, round in cross-section; dorsal surface mottled with red pigment.	Head capsule present, broad; mouthparts reduced; anterior and posterior prolegs absent; last segment with bristles; body curved, round in cross-section; pharyngeal skeleton with several combs, principal comb of angulus undivided.	Not adequately known.	Head capsule present; narrow; mouthparts reduced; anterior and posterior prolegs absent; last segment with bristles; body round in cross-section; pharyngeal skeleton, with three combs, principal comb of angulus divided.	As for *Palpomyia.*
Free from larval exuviae; respiratory trumpet elongate, tubular with a constriction at base; segments 3–7 similarly bristled; anal segment without a bristle-tubercle.	Not adequately known. In *Alluaudomyia* free from larval exuviae; respiratory trumpet funnel-shaped, covered with scales.	As in *Culicoides.*	Not adequately known.	Free from larval exuviae; respiratory trumpet clavate, with numerous spiracles; segments 3–7 similarly bristled; anal segment with a bristle-tubercle; operculum with one pair of setae.	As for *Palpomyia* but in known pupae more than one pair of setae on operculum.
Harpes slender and tapering with variously shaped extremities; ninth sternite emarginate; ninth tergite usually with a sharply pointed process at each posterolateral angle; anal segment membranous with a pair of hairy tubercles which may project beyond the margin of the ninth tergite; phallosome V- or Y-shaped.	Harpes paired, robust, either tapering or ending bluntly.	Harpes paired, robust, blunt or pointed at extremity but not attenuated, fused on mid line in some species of *Monohelea.*	Not adequately known.	Style simple; harpes fused into a single structure or less commonly distinctly separated, although they may be connected at base.	As for *Palpomyia.*

TABLE 2.

Differentiation of the Ceratopogonidae into Groups on Characters found in the Larvae, Pupae and Male Genitalia.

	Group *Leptoconops.*	Group *Atrichopogon.*	Group *Forcipomyia.*	Group *Dasyhelea.*
Occurrence in Australasian Region.	Present.	Present.	Present.	Present.
Genera known to occur in Australasian Region.	*Leptoconops, Styloconops.*	*Atrichopogon.*	*Forcipomyia, Lasiohelea, Pterobosca, Apelma, ? Thyridomyia.*	*Dasyhelea.*
Larvae.	Head capsule not chitinized; mouth parts reduced; without prolegs or anal bristles; pharyngeal skeleton with apparently only one comb.	Head capsule present; mouth parts well developed; with anterior and posterior prolegs; all body segments with short spines; anal segment with double row of hooks; body flattened, transversely oval in cross-section; lateral processes at least as long as segment; pharyngeal skeleton with about six combs, angulus with bristles.	Head capsule present; mouth parts well developed; with anterior and posterior prolegs; body segments with short spines; body segments circular in cross-section; pharyngeal skeleton with about six combs, angulus with bristles.	Head capsule present, short and thick; mouth parts well developed; anterior prolegs absent, last segment with retractile proleg with 10–12 hooks; body curved; pharyngeal skeleton with about six combs, angulus with well developed teeth.
Pupae.	Segments 3–7 similar; anal segment with tubercles, terminal processes simple; respiratory trumpets elongate, ending in a short ovate or barrel-shaped structure with about 10 spiracles.	With larval exuviae attached to last three segments; respiratory trumpets short, knob-like; abdominal segments with branched or setaceous projections on first five.	Similar to *Atrichopogon* but with spines or stump-like projections on all but last segment.	Free from larval exuviae; respiratory trumpets elongated; abdominal segments 2–7 similarly bristled; anal segment in addition to the two apical processes with at least one pair of protuberances.
Male genitalia.	Styles apically bifid or trifid. (Imperfectly known.)	Harpes lacking, or perhaps membranous; ninth sternite narrow, posterior margin emarginate; ninth tergite long, posterior margin rounded, usually without notch; phallosome usually about as broad as long, more or less shield-shaped.	Harpes slender, tapering, often attenuated distally, these may be connected anteriorly at the base by a transverse rod or plate. In *Apelma* the structure is more compact, the distally projecting processes very short. In a few species these processes appear to be lacking, only the transverse bar remaining visible as in some species of *Lasiohelea.*	Harpes in most cases asymmetrical, ninth sternite in some cases emarginate, more often with a central posterior extension; ninth tergite rather long, tapering, with a finger-like process on each latero-posterior angle; phallosome broad; styles either simple or with a basal branch.

to do this with Patagonian species of *Palpomyia*, and a similar difficulty faced de Meillon (1936, p. 187) also with a species from South Africa placed by him in *Palpomyia*. No excuse seems necessary, then, if a similar procedure is occasionally adopted in this revision.

Divisions of the Family.

Fortunately certain groups of genera are sufficiently discrete to be recognizable with some ease. These groupings were even accorded subfamily rank by Enderlein (1936), who recognized the following subfamilies: Leptoconopinae, Forcipomyinae, Ceratopogoninae, Palpomyiinae and Bezziinae. Macfie (1940) considered that apart from the Leptoconopinae all the other subfamilies are untenable because of the common occurrence of annectant forms between them. Nevertheless some form of grouping is necessary, and whether Enderlein's five subfamilies or the nine groups proposed by Macfie are adopted depends largely on their practicability.

Johannsen (1943) has also subdivided the family in a very similar way to Macfie, but divides one of Macfie's groups into two (*Forcipomyia* into *Atrichopogon* and *Forcipomyia* groups) and combines two of Macfie's groups in one (*Palpomyia* and *Bezzia* groups). For our purposes it seems most suitable to accept the first of these differences from Macfie's division, but to disregard the latter. In this way we have the family divided into ten distinct groups, eight of which are known to occur in the Australasian region. Reference to Table 2 will indicate the genera so far recognized from our region and the groups to which they belong as well as the differential characters of each group as found in the larval and pupal forms, and also in the male genitalia. The more obvious characters of the adults are discussed in the text below.

The groups (named after the principal genus) are as follows: (1) *Leptoconops* group, (2) *Forcipomyia* group, (3) *Atrichopogon* group, (4) *Dasyhelea* group, (5) *Culicoides* group, (6) *Ceratopogon* group, (7) *Stilobezzia* group, (8) *Macropeza* group, (9) *Palpomyia* group, and (10) the *Bezzia* group. The first of these, the *Leptoconops* group, is quite discontinuous from the rest of the family and is obviously deserving of subfamily status, although it is not at present feasible to adopt this status when the splitting of the remainder of the family into groupings of similar status cannot yet be accomplished satisfactorily.

TABLE 3.

Major Divisions of the Ceratopogonidae.

First Division. (*Leptoconops* Group.)	Second Division. (*Forcipomyia*, *Atrichopogon*, *Dasyhelea*, *Culicoides* and *Ceratopogon* Groups.)	Third Division. (*Stilobezzia*, *Macropeza*, *Palpomyia* and *Bezzia* Groups.)
Body short, not hairy.	Body comparatively short and hairy.	Body more slender and much less hairy.
Antennae with 12–14 segments.	Antennae with 15 segments.	Antennae with 15 segments.
Broad, bare wings.	Broad and usually hairy wings.	Narrow, bare wings.
Costa short, radial cells not distinguishable, r-m absent, anal vein straight, anal area large.	Costa often short, second radial cell often reduced in length, r-m present, anal vein straight, anal area large.	Costa reaching well beyond middle of wing, second radial cell long, r-m present, anal vein bent at the middle, anal area often reduced.
Lateral piece of scutum (paratergite) narrow.	Lateral piece of scutum (paratergite) narrow.	Lateral piece of scutum (paratergite) relatively broad.
Unchitinized portion of anepisternum narrow and oblique.	Unchitinized portion of anepisternum large and vertical.	Unchinitized portion of anepisternum narrow and oblique.
Femora and claws unmodified.	Femora and claws unmodified.	Femora, or claws, or both variously modified.
Species attacking man.	Many species attacking man and other vertebrates but some species attack other insects.	All species apparently predatory on other insects. No blood-sucking species.

Edwards (1926) divided the Ceratopogonidae, exclusive of the *Leptoconops* group, into two main groups, which he distinguished on a number of characters, a consideration of which is undoubtedly of assistance when attempts to sort specimens are made with the limited data available in Macfie's key to groups (1940, p. 13). Adding the *Leptoconops* group as a separate division, Edwards' division would be roughly as detailed in Table 3.

FIRST DIVISION.

Leptoconops Group.

This is a compact group in which four genera are recognized by Macfie but only two of these are known to occur in the Australasian region. They are primarily differentiated from all other Ceratopogonids by the absence of the r-m cross vein and the reduction of the antennal segments in the female to from twelve to fourteen. The appearance of the antennae with the majority of the flagellar segments short and broad and only the apical one differentiated is reminiscent of the Simuliidae, but the wing venation is distinctive. All branches of the radius fuse in such a way that there are no distinct radial cells and the radius terminates at or before the middle of the wing. Between the radius and the media is found a vein-like thickening extending from the base of the wing to the distal margin* (see Text-figure 4). *Leptoconops* and *Styloconops* are the two genera known to occur in our region.

(*All other Ceratopogonidae have the r-m cross vein present and the female antennae have fifteen segments.*†)

SECOND DIVISION.

Forcipomyia Group.

The presence of a well-developed empodium between the claws of both sexes (in the female only in *Apelma*) distinguishes both the *Forcipomyia* and *Atrichopogon* groups from all the other Ceratopogonids.

In the *Forcipomyia* group there are abundant macrotrichia covering the greater part of the wing. These are recumbent and often scale-like. The radius terminates at about the middle of the wing and the first radial cell is very narrow and often obliterated. The scutum is generally hairy all over. The genus *Lasiohelea* is included in this group although it is in some respects intermediate between *Forcipomyia* and *Atrichopogon*, but the appearance of the wings is such that confusion with *Atrichopogon* is unlikely. Of the genera included in this group, *Forcipomyia*, *Lasiohelea*, *Apelma* and *Pterobosca* have been definitely recognized in the Australasian region. Other genera may still be found, in particular perhaps *Thyridomyia* and *Lepidohelea*.

Atrichopogon Group.

This group comprises species in which the macrotrichia of the wings are comparatively sparse and suberect with the radius extending beyond the middle of the wing, usually to about two-thirds from the base and with both radial cells distinct, the second being two or more times the length of the first (see Text-figure 6). The scutum is bare, or with only short fine hairs.

(*All the remaining groups have the empodium rudimentary and inconspicuous.*)

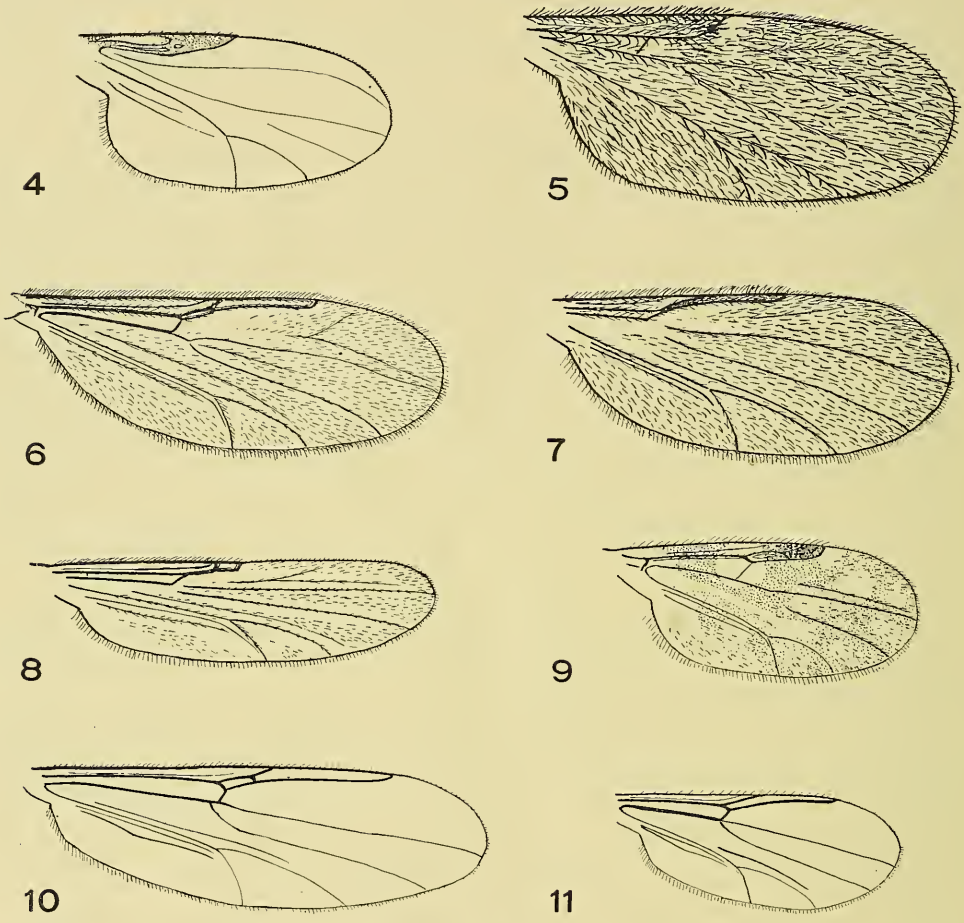
Dasyhelea Group.

In the wings of members of this group the first radial cell is more or less obliterated, the second, if open, is oblong or square, and R_{4+5} is characteristically square-ended or at least sharply angled at the end, and terminates at about the middle of the wing (see Text-figure 8). Macrotrichia are present, sometimes covering the greater part of the wing, sometimes restricted to the distal portion, but in most

* The interpretation of the venation is discussed in greater detail in Part II of this series.

† Occasional reductions in number of antennal segments have been recorded—e.g., *Lasiohelea natalia* de Meillon has eleven segments in the female antennae and fifteen in the male.

species macrotrichia are characteristically absent for a short distance on either side of all wing veins (see Text-figure 8).



Text-figures 4-11.—Typical wings of various genera. Text-figure 4. *Styloconops*. Text-figure 5. *Forcipomyia*. Text-figure 6. *Atrichopogon*. Text-figure 7. *Lasiohelea*. Text-figure 8. *Dasyhelea*. Text-figure 9. *Culicoides*. Text-figure 10. *Palpomyia*. Text-figure 11. *Bezzia*. (For *Stilobezzia* see Text-figure 3.) Various magnifications.

Culicoides Group.

Most species of this group have spotted wings (Text-figure 9), a feature not commonly found in other groups. Usually both radial cells are distinct and subequal, and R_{4+5} terminates at or beyond the middle of the wing, but usually before the level of the end of Cu_1. Microtrichia are distinct and macrotrichia are present, even if only at the apex of the wing. A pair of humeral pits are present anteriorly on the scutum (Text-figure 23). The female claws are equal and small (Text-figure 19).

Ceratopogon Group.

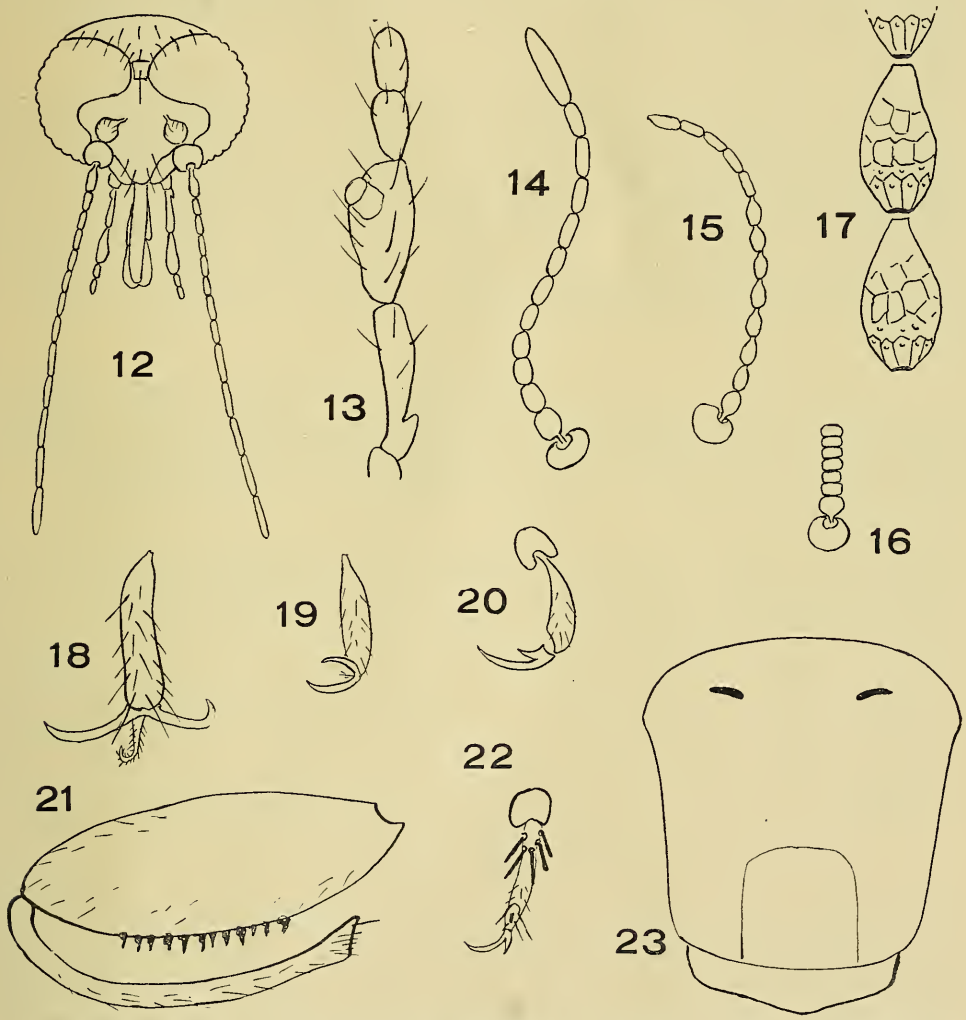
This group is closest to Culicoides. Microtrichia may be present or absent, but if macrotrichia are present they are restricted to the wing tip. The two radial cells are small and subequal and R_{4+5} terminates beyond, but not far beyond, the middle of the wing. Humeral pits are usually distinct and the tarsal claws are large but may be equal or unequal. For further details concerning this group see below (page 329).

THIRD DIVISION.

The members of this division are in the main large species on the wings of which macrotrichia are absent or sparse, the radial veins are clearly defined and R_{4+5} terminates well beyond the middle of the wing. The body is relatively free of hairs and there are modifications in the form of spines, unusual shape or enlargement of the femora, tarsi or claws.

Stilobezzia Group.

In this group the median fork is always petiolate (Text-figure 3), a feature which distinguishes it from all the succeeding groups. There are usually two



Text-figures 12-23.—Various structures mentioned in the key to genera. Text-figure 12. Anterior view of head of *Culicoides*. Text-figure 13. Enlarged palpus of *Culicoides*. Text-figure 14. Antennal segments 2-14 of *Leptoconops*. Text-figure 15. Antennal segments 2-15 of *Forcipomyia*. Text-figure 16. Transverse basal antennal segments of *Apelma*. Text-figure 17. Sculpturing on antennal segments of *Dasyhelea*. Text-figure 18. Fifth tarsal segment of *Forcipomyia* showing empodium. Text-figure 19. Fifth tarsal segment of *Culicoides* showing hair-like empodium. Text-figure 20. Fourth and fifth tarsal segments of *Stilobezzia*. Text-figure 21. Anterior femur and tibia of *Heteromyia*. Text-figure 22. Fourth and fifth tarsal segments of *Xenohelea*. Text-figure 23. Dorsal view of thorax of *Culicoides* showing humeral pits. Various magnifications.

well-defined radial cells, of which the second is considerably longer than the first. Macrotrichia may be present on the distal portion of the wing and an intercalary fork is usually distinguishable. Modifications of the legs are various in the different genera of the group. The genera known to occur in the Australasian region are *Stilobezzia, Acanthohelea* and *Monohelea.*

(*In the remaining groups the median fork is sessile.*)

Macropeza Group.

The shape of the thorax as seen in dorsal view distinguishes this group from all the others. The thorax is distinctly narrowed anteriorly, even sharply pointed, and hence appearing rather conical and in some species even projecting well over the dorsal surface of the head. The group is not known to be represented in the Australasian region.

Palpomyia Group.

The major distinguishing features of this group are the normally anteriorly rounded thorax and the presence of R_{2+3} and hence two distinct radial cells, the second being considerably longer than the first, with R_{4+5} terminating well beyond the middle of the wing (Text-figure 10). Macrotrichia are absent. There may be a small spine or tubercle at the middle of the anterior margin of the scutum, and the legs are modified in various ways in different genera. In our region a number of genera of this group have been recognized, namely, *Palpomyia, Clinohelea, Heteromyia, Xenohelea, Johannsenomyia* and *Dicrohelea.*

Bezzia Group.

In this group R_{2+3} is absent (Text-figure 11) and hence there is only a single long radial cell. This together with the sessile median fork should serve to distinguish the group. So far two genera have been recognized from the Australasian region, namely, *Bezzia* and *Nilobezzia*, but for further details see Part III of this series.

KEY TO GENERA* OF CERATOPOGONIDAE KNOWN TO OCCUR IN THE AUSTRALASIAN REGION.

1. Cross-vein r-m absent (Text-figure 4). Eyes very widely separated. Female antennae with 12-14 segments only (14 in both Australasian genera) (*Leptoconops* Group) .. 2
   Cross-vein r-m present (Text-figures 5-11). Eyes not widely separated (Text-figure 12). Female antennae with 15 segments 3
2. Lamellae of female ovipositor elongate and tapering, equal in length to apical three segments of abdomen ..... *Leptoconops*
   Lamellae of female ovipositor very short, not tapering, their length comparable to that of the terminal abdominal segment ..... *Styloconops*
3. Empodium present and obvious in claws of female and usually in those of male (Text-figure 18) 4
   Empodium lacking or inconspicuous and hair-like in claws of both sexes (Text-figure 19) 9
4. Microtrichia conspicuous, macrotrichia sub-erect, not scale-like and often not covering greater part of wing surface, R_{4+5} always reaching well beyond middle of anterior margin of wing, radial cells distinct, the second longer than the first (Text-figure 6) .... *Atrichopogon*
   Microtrichia minute, macrotrichia abundant, covering greater part of wing surface, recumbent and scale-like, R_{4+5} often terminating about middle of anterior margin of wing, radial cells not usually distinct (Text-figures 5 and 7) .. (*Forcipomyia* Group) .. 5
5. Second radial cell longer than the first and very narrow, R_{4+5} terminating beyond middle of anterior margin of wing (Text-figure 7) ..... *Lasiohelea*
   Second radial cell not obviously longer than the first (if not obliterated), R_{4+5} terminating about the middle of the anterior margin of wing 6
6. Antennae of female with last 6 segments elongate. Empodium large and broad, modified for clinging ..... *Pterobosca*
   Antennae of female with only 5 segments elongate. Empodium not excessively developed 7

* The following genera have, at one time or another, been recorded from Australia or New Guinea, but for various reasons these records are now regarded as incorrect, usually because the species concerned have been found to belong to other genera: *Ceratopogon, Brachypogon* and *Sphaeromias.*

7. Antennae of female with basal flagellar segments (4-10) transverse, short and broad, often with the first few broader than long (Text-figure 16) 8
Antennae of female with basal flagellar segments (4-10) relatively longer, not transverse but round, vasiform or flask-shaped (Text-figure 15) ..... *Forcipomyia*
8. Male without empodium ..... *Apelma*
Male with empodium developed as in female ..... *Thyridomyia**
9. R_{4+5} terminating at middle of anterior margin of wing, first radial cell usually obliterated, second radial cell short and square-ended, macrotrichia usually reasonably abundant (Text-figure 8). Antennal segments sculptured (Text-figure 17) ..... *Dasyhelea*
R_{4+5} terminating beyond, and usually well beyond, middle of anterior margin of wing, radial cells otherwise conformed, macrotrichia abundant, sparse or absent. Antennal segments not sculptured 10
10. M_2 with its origin distal to r-m (median fork petiolate, e.g., Text-figures 3 and 9) 11
M_2 with its origin proximal to, or immediately beneath r-m (median fork sessile) (Text-figures 10 and 11) 14
11. Wings short in relation to width (usually about 2·2, sometimes up to 2·5 times as long as wide), radial cells usually small and subequal, usually partially obscured by a dark spot, rest of wing often conspicuously spotted, microtrichia obvious, macrotrichia dense to very sparse (Text-figure 9). Humeral pits obvious (Text-figure 23). Claws of female equal and small on all legs (Text-figure 19) ..... *Culicoides*
Wings longer in relation to width (usually about 3 times as long as wide, in small species down to 2·5 times), radial cells well developed with the second usually considerably longer than the first, microtrichia not always obvious, macrotrichia restricted to distal portion of wing or absent, wings seldom spotted (Text-figure 3). Humeral pits usually inconspicuous. Claws of female not equal and small on all legs (*Stilobezzia* Group) 12
12. All femora armed with spines ..... *Acanthohelea*
All femora without spines 13
13. Femora of hind legs thickened. Claws of female unequal on hind legs only .. *Monohelea*
Femora of hind legs not thickened. Claws of female unequal on all legs (Text-fig. 20) ..... *Stilobezzia*
14. R_{2+3} present, hence two distinct radial cells 15
R_{2+3} absent, only one radial cell (Text-figure 11) 20
15. Fifth segments of tarsi not armed with strong spines 16
Fifth segments of tarsi armed with strong spines (Text-figure 22) 18
16. Fifth tarsal segments of forelegs inflated; fourth tarsal segments of four posterior legs bilobed and armed with spines, femora unarmed ..... *Clinohelea*
Fifth tarsal segments of forelegs not inflated; fourth tarsal segments not armed, femora armed 17
17. Femora of forelegs greatly swollen with fore tibiae strongly curved to the outline of the femora (Text-figure 21) ..... *Heteromyia*
Femora of forelegs normal or if swollen then not to such an extent that the tibiae are curved to fit the outline of the femora ..... *Palpomyia*
18. Claws of female equal and barbed on forelegs, unequal and barbed on four posterior legs ..... *Dicrohelea*
Claws of female otherwise 19
19. Claws of female unequal and simple on all legs (Text-figure 22) ..... *Xenohelea*
Claws of female all equal and barbed ..... *Johannsenomyia*
20. Femora of at least the forelegs armed with stout spines; fifth tarsal segments not armed ..... *Bezzia*
Femora without stout spines, at most spinules (strengthened hairs) present on four posterior legs; fifth tarsal segments armed with strong spines ..... *Nilobezzia*

Genus Ceratopogon Meigen.
(Including *Brachypogon* Kieffer.)

Despite the fact that Skuse (1889) placed all of his species except one in the genus *Ceratopogon* and Kieffer (1917) allocated ten species to this genus, including five of Skuse's species and one of Schiner's, and a further one of Skuse's species to the genus *Brachypogon*, there is still no evidence that the genus, as it is now understood, occurs in Australia.† Most of the species retained in *Ceratopogon* by Kieffer really belong

* The genus *Thyridomyia* does not necessarily occur in the Australasian region but is included here in case of possible confusion with *Apelma*, when only female specimens may be available. For practical purposes it would perhaps be best to regard *Apelma* and *Thyridomyia* as merely subgenera of *Forcipomyia*.

† Edwards (1928) described *Ceratopogon* (*Isohelea*) *peregrinator* from Savaii (Samoa), so it seems possible that *Ceratopogon* may eventually be found westward of Samoa, at least in the tropical part of the region.

to the genus *Forcipomyia*, due to Kieffer's misconception of the genotype of *Ceratopogon* (see Edwards, 1926, page 407), and a few are obviously species of *Atrichopogon*. Only one species has really remained in doubt, and that is Skuse's *Ceratopogon imperfectus*, usually called by Kieffer *Brachypogon imperfectus*. My preliminary examination of the type specimen, mounted in gum on a card, left me in doubt as to which genus this species really belonged, since little beyond the wing venation could be made out in the specimen. However, on remounting in euparal it was immediately obvious that the specimen belonged to the Chironomidae and not the Ceratopogonidae at all, and should now be called *Spaniotoma* (*Smittia*) *imperfectus*.

It should be noted that in the one publication Kieffer (1906) placed this same species in both *Chironomus* (p. 19) and *Brachypogon* (p. 59), but in his 1917 revision he mentions it only in the genus *Brachypogon*.

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